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Smooth skate (*Malacoraja senta*) in the southern Gulf of St. Lawrence: life history, and trends from 1971-2010 in abundance, distribution and potential threats

Situation de la raie lisse (*Malacoraja senta*) dans le sud du golfe du Saint-Laurent : caractéristiques du cycle de vie, les tendances dans l'abondance et la distribution depuis 1971 à 2010, et les menaces potentielles

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ABSTRACT

An assessment by the Committee on the Status of Endangered Wildlife in Canada of the status of smooth skate (*Malacoraja senta*) in Canadian waters in terms of its risk of extinction is scheduled for 2012. This document presents information on life history traits, trends in the abundance and distribution of this species, and threats to its persistence in the southern Gulf of St. Lawrence. A bottom-trawl survey, conducted each September since 1971, is the main source of information on the abundance and distribution of smooth skate in this area. Smooth skate occur in relatively deep areas of the southern Gulf, with highest densities occurring between depths of 150 and 300 m. There is little geographic segregation evident between length classes of smooth skate, and little seasonal variation in their geographic distribution in this area. There has been no long term trend in the area occupied by adult smooth skate (defined here as skates ≥ 48 cm in total length) over the 1971-2010 period. The area occupied by juveniles was smaller in the late 1970s and early 1980s than it has been since the late 1980s. Trends in abundance also differ between juvenile and adult skates. Survey catch rates of juveniles tended to be relatively high in the 1990s compared to the period from the mid 1970s to the early 1980s. In contrast, survey catch rates of adults declined from relatively high levels in the 1970s to very low levels in the early 2000s, with an increase in recent years. The above average abundance of juveniles throughout much of the 1990s and 2000s despite below average spawner abundance suggests that juvenile mortality was relatively low during this period. The below-average adult abundance throughout much of the 1990s and 2000s despite strong recruitment suggests that adult mortality was relatively high during this period. The two main threats to smooth skate in the southern Gulf are likely fishing and predation. There are no directed fisheries for skates in the southern Gulf but skates are incidentally captured in fisheries targeting other species. Most skates are discarded at sea. From 1991-2010, discards comprised on average 95% of total estimated smooth skate catches. Estimated annual discards of smooth skate declined from a peak of around 180 tonnes in the early 1990s to about 25 t in the late 2000s. This decline is likely due in part to the reduction in fishing effort in the southern Gulf over this period. The apparent low mortality of juveniles in the 1990s and 2000s may reflect release from predation following declines in the biomass of large demersal fish in this area beginning in the early 1990s. The apparent high mortality of adults in the 1990s and 2000s despite decreasing fishing effort may be partly due to increased predation by the growing grey seal herd in this area.

RÉSUMÉ

Une évaluation par COSEPAC (comité sur la situation des espèces en péril au Canada) de l'état de la raie lisse dans les eaux canadiennes quant à son risque d'extinction est prévue pour 2012. Ce document présente de l'information sur les caractéristiques du cycle de vie, les tendances dans l'abondance et la distribution de cette espèce et les menaces à sa continuité dans le sud du golfe du Saint-Laurent. Un relevé au chalut de fond, mené annuellement au mois de septembre, est la principale source d'information sur l'abondance et la distribution de cette espèce dans cette région. La raie lisse se retrouve dans les régions relativement profondes du sud du Golfe et on retrouve les plus grandes densités à des profondeurs de 150 et 300 m. Il y a peu de séparation géographique perceptible entre les classes de longueurs de la raie lisse et il y a peu de variation saisonnière de leur distribution géographique dans cette région. Il n'y a eu aucune tendance à long terme quant à la région occupée par les raies lisses adultes (défini ici comme des raies ≥ 48 cm de longueur totale) durant la période de 1971-2010. La région occupée par les raies juvéniles était plus petite à la fin des années 1970 et au début des années 1980 qu'elle l'est depuis la fin des années 1980. Les tendances dans l'abondance diffèrent également entre les raies adultes et juvéniles. Le taux de capture des raies juvéniles du relevé était relativement haut dans les années 1990 en comparaison avec la période du milieu des années 1970 au début des années 1980. À l'opposé, le taux de capture des raies adultes a diminué d'un niveau relativement haut dans les années 1970 à un niveau très bas au début des années 2000, mais a été suivi d'une augmentation dans les récentes années. L'abondance moyenne des raies juvéniles durant la majorité des années 1990 et 2000, mentionnée ci-dessus, suggère une mortalité chez les juvéniles relativement basse durant cette période, malgré le fait que l'abondance des reproducteurs était en-dessous de la moyenne. Malgré un recrutement élevé, l'abondance en-dessous de la moyenne des raies adultes tout au long des années 1990 et 2000 suggère une mortalité relativement élevée des raies adultes durant cette période. Les deux principales menaces de la raie lisse dans le sud du Golfe sont probablement la pêche et la prédation. Il n'y a pas de pêche directe sur la raie lisse dans le sud du Golfe, mais les raies sont capturées incidemment par des pêches visant d'autres espèces de poisson. La plupart des raies sont rejetées à la mer. De 1991 à 2010, les raies rejetées à la mer correspondaient en moyenne à 95% de l'estimation totales des captures de raies lisses. L'estimation des rejets annuels de raies lisses a diminué d'un sommet à 180 tonnes au début des années 1990 à environ 25 tonnes à la fin des années 2000 (fig. 18). Cette diminution est probablement causée par la réduction de l'effort de pêche dans le sud du Golfe durant cette période. La basse mortalité des juvéniles dans les années 1990 et 2000 est peut-être le reflet d'un relâchement de la prédation puisqu'il y a déclin dans la biomasse des grands poissons démersaux dans cette région depuis le début des années 1990. La mortalité élevée des raies adultes dans les années 1990 et 2000, malgré la diminution de l'effort de pêche, pourrait être partiellement due à l'augmentation de la prédation par les troupeaux grandissant de phoques gris dans la région.

INTRODUCTION

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has chosen to evaluate the status of the smooth skate (*Malacoraja senta*) in Canadian waters in terms of risk of extinction. The purpose of this paper is to provide information on life history traits and trends in the abundance, distribution and potential threats of this species in the southern Gulf of St. Lawrence. Further details can be found in Swain et al. (2005) and Kulka et al. (2006).

DATA SOURCES – LIFE HISTORY, DISTRIBUTION AND ABUNDANCE

Data are from annual bottom trawl surveys conducted in the southern Gulf of St. Lawrence each September since 1971. Surveys used a stratified random design, with stratification based on depth and geographic region (Fig. 1). During these surveys, trawling was conducted at 63-74 sites in each year from 1971-1983, 82-132 sites in 1984-1988, and about 140-200 sites in 1989-2010 (except 2003, when only 83 stations were successfully fished). The target fishing procedure in all years was a 30-min tow at 3.5 knots. All catches were adjusted to a standard tow of 1.75 nautical miles.

Survey coverage was expanded in 1984 to include three inshore strata (401-403). Analyses presented here are restricted to the 24 strata fished since 1971 (strata 415-439). Of these 24 strata, two (424 and 428) were not fished in 1978, while stratum 421 was not fished in 1983 and 1988. In order to maintain a consistent survey area, in the years when these strata were not fished their weights were added to those of neighboring strata in the same depth zone in calculations of stratified mean catch rates and distribution indices. For example, in 1978, half the weight associated with stratum 424 was apportioned to stratum 423 and half was apportioned to stratum 422. In 2003, no stations were fished in strata 438 and 439. In this case, predicted values for the mean catch rate in these strata were obtained using generalized linear models with terms for year and stratum. Models used a log link and assumed a Poisson error distribution allowing for overdispersion. This analysis was restricted to the 2002 – 2004 period to avoid effects of changes in distribution.

The research vessels conducting the survey were the *E. E. Prince* from 1971 to 1985, the *Lady Hammond* in 1985 to 1991, the *Alfred Needler* in 1992 to 2002, the *Wilfred Templeman* in 2003, both the *Alfred Needler* and the *Teleost* in 2004 and 2005, and the *Teleost* in 2005-2010. Tows conducted by the *E. E. Prince* used a Yankee 36 trawl; all other vessels used a Western IIA trawl. Relative fishing efficiency for smooth skate between these vessels and gears was estimated from comparative fishing experiments conducted during or shortly before the September survey in 1985, 1992, and 2004/2005. These experiments failed to detect any differences in fishing efficiency for smooth skate between these vessels and gears (Benoît and Swain 2003; Benoît 2006b). No comparisons were conducted with the *Wilfred Templeman* using a Western IIA trawl.

Fishing was conducted only during daylight hours (07:00-19:00) in 1971-1984 but 24-h per day since 1985. Catches were adjusted for diel differences in fishing efficiency, as described in Benoît and Swain (2003). Smooth skate had higher catchability at night than in day, and night catches were adjusted to be equivalent to day catches. These adjustments were independent of fish length (Benoît and Swain (2003) for details). Because there were no differences in fishing efficiency for smooth skate between the *Alfred Needler* and the *Teleost* (Benoît 2006b), the diel difference in catchability for the *Teleost* was assumed to be the same as that estimated for the *Alfred Needler*.

LIFE HISTORY

Maturity has been staged for length-stratified subsamples of skate catches during the September survey since 2005. Descriptions of the maturity stages used are given in Appendix I. Fish classified as being at stages 4 and 5 were considered mature in the analyses below. Estimated lengths at 50% maturity were 47.0 cm ($N=151$) for males, and 45.2 cm ($N=179$) for females (Fig. 2). At a zonal review of information on smooth skate in Atlantic Canada held in October 2006 (DFO 2006), it was decided that 48 cm would be used as the length demarking mature (≥ 48 cm) versus immature (<48 cm) individuals for all regions. The estimated lengths at 50% maturity for smooth skate in the southern Gulf are close to this value, and 48 cm was retained for the analyses presented here.

GEOGRAPHIC DISTRIBUTION AND HABITAT ASSOCIATIONS

METHODS

The geographic distribution of skates was mapped using the data visualization software ACON (<http://www.mar.dfo-mpo.gc.ca/science/acon>). Shaded contours were drawn using Delaunay triangles.

Area of occupancy (A_t) was calculated for each size class of skates in year t as follows:

$$A_t = \sum_{k=1}^S \sum_{j=1}^{N_k} \sum_{i=1}^{n_j} \frac{a_k}{N_k n_j} I \quad \text{where } I = \begin{cases} 1 & \text{if } Y_{ijkl} > 0 \\ 0 & \text{otherwise} \end{cases} \quad (1)$$

where N_k is the number of sites sampled in stratum k , n is the number of tows undertaken at site j in stratum k , a_k is the area of the stratum k and Y_{ijkl} is the catch of smooth skate in size-class l in tow i at site j and stratum k .

Area of occupancy (as defined above) will decrease as population size decreases even if there is no increase in geographic concentration (Swain and Sinclair 1994). In order to describe changes in geographic concentration, for each size class of skates we also calculated the minimum area containing 95% of skates, following Swain and Sinclair (1994). First, we calculated catch-weighted cumulative distribution functions (cdf's) of skate catch in each year:

$$F(c) = 100 \frac{\sum_{i=1}^n w_i y_i I}{\sum_{i=1}^n w_i y_i} \quad \text{where } I = \begin{cases} 1 & \text{if } y_i \leq c \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

where c is a level of skate catch (i.e., number per standard tow), w_i is the weighting factor for tow i (i.e., the proportion of the survey area in the stratum fished by tow i divided by the number of tows made in that stratum), n is the number of trawl tows in the survey, and y_i is the number of skates caught in tow i . $F(c)$ is an estimate of the percent of skates that occur at a local density of c or less. We also calculated cumulative area in relation to skate catch:

$$G(c) = \sum_{i=1}^n \alpha_i I \quad \text{where} \quad I = \begin{cases} 1 & \text{if } y_i \leq c \\ 0 & \text{otherwise} \end{cases} \quad (3)$$

where α_i is the area of the stratum fished by tow i divided by the number of tows made in that stratum. F was evaluated at intervals of 0.01, the density c_{05} corresponding to $F = 5$ was calculated. $G(c)$ is the estimated area containing the most sparsely distributed 5% of skates (including areas where no skates were caught). Thus, the minimum area containing 95% of skates (D_{95}) is given by:

$$D_{95} = A_s - G(c_{05}) \quad (4)$$

where A_s is 70 075 km², the total survey area.

We examined variation in the habitat associations of smooth skate using cumulative distribution functions (Perry and Smith 1994) and generalized additive models (GAMs; Hastie and Tibshirani 1990). A Poisson error distribution was assumed in the GAMs, allowing for overdispersion. Models were of the form:

$$E[Y_i] = \mu_i = \exp(\beta_0 + s(X_i)) \quad (5)$$

$$\text{Var}[Y_i] = \phi\mu_i \quad (6)$$

where Y_i is the catch of skates in tow i , and $s(X_i)$ is a cubic spline function of depth. We specified the degree of smoothing for the depth term by setting its degrees of freedom to 4.

RESULTS

In September, smooth skate in the southern Gulf of St. Lawrence are distributed in relatively deep waters in the Cape Breton Trough and along the slope of the Laurentian Channel (Fig. 3). Little geographic segregation is evident between length classes of smooth skate in this area (Fig. 4). Previous studies indicate that there is little seasonal variation in the geographic distribution of smooth skate in this area (Clay 1991; Darbyson and Benoit 2003).

Trends in area occupied in September differed between juveniles and adults (Fig. 5). For juveniles, area occupied averaged less than 2000 km² in the late 1970s, increasing in the early 1980s to values near 4000 to 6000 km² from the mid 1980s to 2010. For adults, area occupied fluctuated widely around an average level near 2500 km² from the early 1970s to the mid 1990s, decreasing to a lower level in the late 1990s and then recovering to a higher level in the 2000s. Trends in D_{95} were similar to the trends in area occupied (Fig. 6). There were no long-term trends in area occupied or D_{95} ; levels of these indices were similar at the start and at the end of the 40-yr time series.

The areas occupied by smooth skate are warmer and deeper than the median bottom temperatures and depths available in the southern Gulf (Fig. 7). Mean and median depths of September survey catches of smooth skate were generally between 125 and 250 m (Fig. 7a). The depth range containing 50% of the skate caught during the survey varied considerably from year to year, but the majority of smooth skate were caught at depths between about 75 and 325 m (Fig. 7a). Little bathymetric segregation by size class is evident in the September survey catches (Fig. 8). The mean temperatures occupied by smooth skate varied between about 2

and 5°C (Fig. 7b; excluding the 1984-1988 period when estimates of occupied temperature are negatively biased due to the lack of temperature measurements in deep waters). No strong interannual trends are evident in the depths and temperatures occupied by smooth skate in September in the southern Gulf.

Depth distribution is summarized within decadal time periods using generalized additive models in Figure 9. In the 1970s, a broad peak in density occurred from about 150 to 250 m. In the 1980s and 1990s, density peaked sharply at about 225 and 175 m, respectively. In recent years (2001 – 2010), density was highest over a broad range of depths (150 – 300 m). In all time periods, densities were very low at depths shallower than about 100 m. Density also declined to low values in the deep water along the offshore edge of the survey area. This decline in density in deep waters was less sharp in the most recent time period, though this mostly reflected the low peak density in this period.

Smooth skate do not have any known dwelling-place similar to a den or nest during any part of their life.

CHANGES IN ABUNDANCE, BIOMASS AND SIZE COMPOSITION

METHODS

Length distributions were determined for each tow in 3-cm intervals. For each year, the stratified mean catch per tow was calculated for each length interval:

$$\bar{Y}_t = \sum_{k=1}^S \sum_{j=1}^{N_k} \sum_{i=1}^{n_j} \frac{w_k}{N_k n_j} Y_{ijkl} \quad (7)$$

where the parameters of the equation are as described for eqn 1. The total stratified mean catch per tow and its standard error in each year was also calculated for two length groups: < 48 cm and ≥ 48 cm in total length (TL). The larger size group corresponds roughly to the mature population. Stratified mean length distributions were also converted to biomass using annual length-weight relationships.

An exponential decay model was also fitted to the time series using the linear regression of $\log_e \bar{Y}_t$ versus t , where \bar{Y}_t is the stratified mean catch rate of adult skate in the survey in year t . Zeros were replaced by half the minimum nonzero value before taking the log. The slope of this regression is the estimated rate of decline (b), and can be used to calculate an estimate of the percent decline over t years (Δ):

$$\Delta = 100 \cdot (1 - e^{-b \cdot t}) \quad (8)$$

RESULTS

Catch rates of smooth skate in the September survey show considerable interannual fluctuations (Fig. 10), likely due in part to the restricted distribution of smooth skate within the survey area. Abundance tended to decline from the mid 1970s to the early 1980s. Abundance increased in the mid 1980s and was relatively high throughout the 1990s. Abundance declined again in the early 2000s but has recovered somewhat since then. Biomass showed similar

trends, though the increases in the 1980s and in recent years were not as substantial as for abundance.

Trends in abundance differed between juveniles and adults (Fig. 11). Juvenile catch rates tended to be high in the 1990s, comparable to the rates observed in the mid 1970s. Adult catch rates were relatively low in the 1990s, less than half the average level observed in the mid-1970s. Catch rates of adults declined to very low levels in the early 2000s but recovered to the 1990s level in the late 2000s.

The linear regression of log adult catch rates versus time was statistically significant, with an estimated average annual decline of about 3% (Fig. 12). This corresponds to a 67% decline over the 40-yr time series. Given the recent increase in adult catch rates to about the 1990s level, it is possible that the decline has ceased.

In the 1970s and 1980s, most smooth skate caught in the September survey were between 20 and 50 cm in length (Fig. 13). Catch rates were highest at about 50 cm. In the early 1990s, catch rates were highest at small sizes, between 10 and 35 cm TL, and were considerably lower at greater lengths. In the late 1990s, catch rates were greatest at somewhat larger sizes, between 25 and 40 cm. In the late 2000s, the size distribution of catches was fairly uniform between lengths of about 10 and 55 cm, with peaks at about 10, 20-25 and 45-50 cm.

POPULATION SIZE

"Trawlable" abundance is the stratified mean catch per standard tow multiplied by the survey area and divided by the area swept by a standard tow. Trawlable abundance is expected to underestimate actual abundance within the survey area because fishing efficiency is very likely less than 100%.

The total survey area (strata 415-439) is 1729346 times the area swept between the trawl wings during a standard 1.75 nm tow. Based on the survey catch rates of adult skate standardized to daytime catchability, estimated trawlable abundance for the mature portion of the population declined from about 125,000 fish in the 1970s to 43,000 fish in the 2000s. Standardizing to nighttime catchability, average estimated trawlable abundance in the 2000s is 104,000 adult skate. Trawlable biomass (all sizes) declined from an average of 140 t in the 1970s to 64 t in the 2000s based on daytime catchability; estimated average trawlable biomass in the 2000s based on night catchability is 154 t.

THREATS

FISHING

Background

There are no directed fisheries for skates in the southern Gulf of St. Lawrence (sGSL; Northwest Atlantic Fisheries Organization division 4T). However, skates are incidentally captured in a number of fisheries (e.g., Benoît 2006a, 2011). Though some skates are landed annually, most are discarded at sea. Skate landings are available directly from Fisheries and Oceans Canada's (DFO) landings database, termed the Zonal Interchange File Format (ZIFF) database. Discarded amounts of skates must be estimated using data collected by fisheries

observers, which are deployed on a subset of commercial fishing trips (typically 5-25% of trips, depending on the fishery (Benoît and Allard 2009)) in all of the fisheries believed to catch thorny and smooth skates in the sGSL. Incidental catches of non-target species in the sGSL snow crab (*Chionoecetes opilio*) fishery are not reported by at-sea observers, though catches of fish are generally very small to nil (pers. comm. M. Lanteigne and P. Degrâce, Fisheries and Oceans Moncton). Incidental catch of skates in fisheries targeting pelagic fish such as herring (*Clupea harrengus*), mackerel (*Scomber scombrus*), and bluefin tuna (*Thunnus thynnus*) are likewise likely to be nil. The sGSL scallop (*Placopecten magellanicus*) fishery catches some winter skate (*Leucoraja ocellata*), but no smooth skate (Benoît 2011). Other important fisheries in the southern Gulf, such as the lobster (*Homarus americanus*) and rock crab (*Cancer irroratus*) fisheries, occur in waters that are too shallow to capture smooth skate, if they catch much skate at all.

Skates are not identified to species in the landings data, and are not consistently or reliably identified to species by the fisheries observers (Benoît 2006a). Three species of skates make up more than 99% of the skate catches in the annual September bottom-trawl survey of the sGSL (Hurlbut and Clay 1990; H. Benoît, unpublished analyses): winter skate, smooth skate, and thorny skate (*Amblyraja radiata*). Fishery catches are attributed to each of these species using an empirical model.

Methods

Predicting the species composition of catches

Depth and season are strong predictors of the relative distribution of many sGSL species, including skates (e.g., Darbyson and Benoît 2003; Benoît 2006a). These variables are available along with the catch information recorded by fisheries observers, allowing species composition of fishery catches to be estimated. Furthermore, because observers report the amounts of fish that are discarded and retained, the approach described below can be used to predict species composition for both landed and discarded portions of the catches.

A multinomial regression model based on baseline-category logits (Agresti 2002, p. 267-274) has been developed and validated to model seasonal changes in the bathymetric distribution of skate species composition in the sGSL (H. Benoît, manuscript in preparation). Given that a skate has been observed, let $\pi_j(d, t) = P(Y = j | d, t)$ be the response probability, i.e., the probability that skate Y is of species j , given that it was caught at depth d (in meters) and at time t (day-of-year). Now define the linear model:

$$\log \frac{\pi_j(d, t)}{\pi_J(d, t)} = \beta_{0,j} + \beta_{1,j} \cdot d + \beta_{2,j} \cdot d^2 + d \cdot \sum_{p=1}^3 \alpha_{p,j} \cdot \sin(p\omega t - \phi_{p,j}), j = 1 \text{ to } J-1 \quad (9)$$

where $\omega = 2\pi/365$ is the fundamental annual frequency, p defines the cycle frequency (annual, $p=1$; semi-annual, $p=2$; tri-annual, $p=3$), $J=3$ is the number of skate species in the sGSL and $\beta_{0,j}$, $\beta_{1,j}$, $\beta_{2,j}$, $\alpha_{p,j}$ (signal amplitude) and $\phi_{p,j}$ (signal phase) are estimated parameters. The three cycle frequencies are those used to model site specific temperature changes in the sGSL (Ouellet et al. 2003), and are therefore also expected to influence species distributions. The left-hand part of eqn 9 is the logit for the response of species j relative to a chosen baseline species J . The choice of baseline species is arbitrary, because $\sum_{j=1}^J \pi_j(d, t) = 1$ and the $J-1$ equations defined

by eqn. 9 therefore determine the parameters required to define the logits of any pair of skate species (Agresti 2002, p. 268).

The multinomial harmonic regression model was fit using the maximum-likelihood method (Agresti 2002, p. 272-274) to unstandardized catches of individual skate captured in the various fishery-independent surveys carried out in the sGSL at different times of the year (Pitt et al. 1981; Hurlbut and Clay 1990; Darbyson and Benoît 2003; Savoie and Surette 2010; Bosman et al. 2011). The model in eqn. 9 was found to fit the observed data well (Fig. 14). The model was also validated by fitting it to survey catches of five sGSL flatfish species and comparing the predictions to catches of these same flatfish species reported by at sea observers, who are assumed to properly and consistently identify flatfish to the species level (H. Benoît, manuscript in preparation).

For a given observed fishing set, k , predicted response probabilities $\hat{\pi}_{j,k}$ were obtained using the logit-transformation of eqn 9:

$$\hat{\pi}_j(d,t) = \frac{\exp(\beta_j' X_k)}{\sum_{h=1}^J \exp(\beta_h' X_k)}, \text{ for } j=1, \dots, J \text{ with } \beta_J = 0 \quad (10)$$

and where $j = J$ is the baseline species and β_j and X_k are shorthand for the vector of parameters for species j and the matrix of explanatory variables for set k , respectively. The expected biomass of skate species j in fishing set k was calculated as:

$$\hat{b}_{j,k} = B_k \hat{\pi}_{j,k} \quad (11)$$

where B_k is the total biomass of skates in the catch (note that observers report catch amounts in mass only) and $b_{j,k}$ is the biomass of species j .

Bycatch estimation

Fourteen fisheries covering eleven commercially important taxa were the target of fishery observer surveys over the period from 1991-2010 and were used to estimate skate bycatch (Table 1). Though observer data for certain years prior to 1991 are available, the proportion of trips covered was small and the information collected deemed not sufficiently reliable to properly estimate skate bycatch (H. Benoît, unpublished analyses).

Fisheries observers record the amounts of both landed skates, R_k , and discarded skates, D_k , in an observed fishing set, k . These data were used to estimate total annual smooth skate bycatch as:

$$\hat{d}_{j,t} = \sum_f \left[\left(\frac{\sum_k B_{f,k,t} \cdot \hat{\pi}_{j,k}}{\sum_k \sum_s C_{s,f,k,t}} \right) \cdot \sum_s L_{s,f,t} \right] \quad (12)$$

where $\hat{d}_{j,t}$ is the estimated bycatch of skate species j (here, smooth skate) in year t , $B_{f,k,t}$ ($= R_{f,k,t} + D_{f,k,t}$) is the biomass of skate reported by observers for fishing set k in fishery f during year t , $C_{s,f,k,t}$ is the retained catch of commercial fish species s reported by observers for the set, and $L_{s,f,t}$ is the landed amount of species s in fishery f and year t taken from landings statistics

contained in DFO's ZIFF database. The estimates were stratified by fishery because this is the level at which decisions on fishery observer allocations are made (Benoit and Allard 2009). Because the location, timing and fishing procedures employed all vary by fishery, stratifying in this manner also accounts for a potentially large source of variability in the relative amounts of incidentally captured and target species in the catch. For the fisheries observer data, fisheries were defined using the 'main species' and 'gear' variables. For the landings data, fisheries were defined using the 'species sought' variable for cases in which it was provided by the harvester and available in the ZIFF database, or the 'main species' variable otherwise, as well as the 'gear' variable. Because observer records were sparse for certain fisheries in certain years, observed sets from the fishery in adjoining years were sometimes used to calculate $\hat{d}_{j,t}$ (details in Table 2). Sparse observer records typically correspond to fisheries and years in which there was little fishing effort and few landings.

Two metrics of smooth skate bycatch were calculated using the data collected by fisheries observers: estimated landings and estimated discards. The estimated landings of smooth skate (here, species j) in year t , $\hat{r}_{j,t}$, was calculated by replacing $B_{f,k,t}$ in eqn. 12 with $R_{f,k,t}$, the amount of skate in set k in fishery f and year t that was reported as being retained by the harvester. Comparing $\sum_{j=1}^3 \hat{r}_{j,t}$ (i.e., sum over the three sGSL skate species) with landings from the official statistics provided a validation of the bycatch estimation process. Furthermore, the estimated species composition for the retained skate catches was used to separate landings by species:

$$\hat{l}_{j,t} = L_{\text{skate},t} \frac{\hat{r}_{j,t}}{\sum_{j=1}^3 \hat{r}_{j,t}} \quad (13)$$

where $\hat{l}_{j,t}$ is the estimated amount of the official skate landings, $L_{\text{skate},t}$, that is comprised of skate species j , in year t .

The amount of skate species j that was discarded in year t , was estimated by replacing $B_{f,k,t}$ in eqn. 12 with $D_{f,k,t}$, the amount of skate in set k in fishery f and year t that was reported by the observers as being discarded.

Error estimation and propagation

Uncertainty in the estimated discards was estimated using empirical bootstrapping for two key aspects of the estimation process (Efron and Tibshirani 1993). Uncertainty in the response probabilities in eqn. 10 was simulated by re-sampling the data used to fit eqn. 9. Survey sets were sampled with replacement from within individual surveys (and years, for multi-year surveys) and within survey strata. Strata in the sGSL are defined largely by depth (e.g., Hurlbut and Clay 1990), and stratifying the bootstrap in this way ensured that re-sampling was representative of the original temporal and depth-distribution of sets. Uncertainty associated with the estimates from eqn. 9 was simulated by randomly selecting with replacement observed fishing sets within fisheries, f , and years, t . One thousand iterations were found to be sufficient to provide stable estimates of uncertainty for the discards.

Results and Discussion

Skate landings in the sGSL have varied considerably over time, peaking at around 130 tonnes in 1975 and 1976, with smaller peaks (20-60 tonnes) occurring in the late 1970s and early

1980s and during the mid to late 1990s (Fig. 15; Table 3). Landings during intervening periods, particularly 1985-1993, were relatively low. For the period over which comparisons can be made, skate landings estimated using observer records of retained catch match reasonably well the official landing statistics (Fig. 16). This helps to validate the observer data and model used to estimate skate catches, and suggests that skate discards are likely to be reliably estimated. Furthermore, this also suggests that eqn. 13 might be used to accurately predict the landings for individual skate species. For smooth skate over the period 1991-2010, landings peaked in the mid 1990s at around 8-16 tonnes, declining thereafter to generally less than 3 tonnes per year, with the exception of a second small peak in 2003-2005 (Fig. 17; Table 3).

From 1991-2010, discards have comprised on average 95% (and no less than 87%) of total estimated smooth skate catches in commercial fisheries (Tables 3 and 4). Discards of smooth skate have declined from a peak of around 180 tonnes in the early 1990s to a low of around 25 in the late 2000s (Fig. 18). The decrease in total catches for smooth skate likely reflects in part the changes in fishing effort that have occurred in the sGSL since 1990 (Fig. 7 in Benoît and Swain 2011). Though the estimation of mean discard levels appears to be validated by the analysis in Figure 16, it is likely that uncertainty in the estimates shown in Figure 18 may have been under-evaluated because of unrepresentative deployment of observers (Benoît and Allard 2009).

Around 40% of estimated smooth skate discards originated from the cod mobile gear fishery prior to the moratorium placed on that fishery in 1993 (Fig. 19). For 1994-1999, the majority of smooth skate discards (~75%) originated from the American plaice and witch flounder mobile gear fishery. Prior to 1998, less than 20% of the discards came from the Greenland halibut gillnet fishery. After 1998, this percentage increased to close to 90% by the mid 2000s, decreasing temporarily in 2007-2008, when estimated discards in mobile gear fisheries targeting other species increased.

Using data collected by fisheries observers on the vitality of skates just prior to discarding (Benoît et al. 2010), the mortality of sGSL skates captured and discarded in mobile gear fisheries has been estimated for two periods, the early 1990s and mid 2000s (Benoît et al. 2012). These periods differ in the intensity of fishing directed at groundfish and in the time it took harvesters to sort their catch and to discard unwanted fish, a key factor in determining whether a discarded fish will die as a result of capture and handling. During the early 1990s the survival rate of skates discarded in sGSL mobile gear fisheries was estimated at 0.51 (0.09, S.E.), while for the mid 2000s the estimated rate was 0.97 (0.02). These estimates do not incorporate indirect post-release mortality resulting from capture and handling, such as enhanced risks of predation or disease, and should therefore be taken as minimal estimates of mortality. There are no estimates of the survival rate for skates discarded in gillnet fisheries, which have been the predominant source of capture for smooth skates during most of the 2000s. Short deck times associated with hauling gillnets means that skates are likely typically returned to the water rapidly, greatly enhancing discard survival potential of skates that are still alive when the nets are hauled (Benoît et al. 2010). Within-net mortality of fish has been associated with soak time and temperature, as well as the configuration of the net (Bettoli and Scholten 2006; Fréchet et al. 2006). The median soak time in the Greenland halibut gillnet fishery, which has been the main source of skate capture in recent years, is 3 days (Sylvain Ménégat, Université du Québec à Rimouski, manuscript in prep). This amount of soak time results in around 35% mortality of Greenland halibut removed from the nets. At the maximum observed soak time of 7-8 days, mortality is close to 70%. Skate survival is expected to be better because they are not vulnerable to occlusion of their spiracles by the net, in contrast to

halibut which are vulnerable to operculum occlusion. The estimates for Greenland halibut might therefore serve as an upper bound for skate mortality.

The average fishery landings for the 2000s (2.3 tonnes/year) represent between 1.5-3.6% of adult trawlable biomass, depending on whether daytime or night time catchability is assumed. During the 2000s, the mean discard estimates of 38.2 tonnes/year would have represented between 25-60% of adult trawlable biomass. The absence of more accurate mortality estimates for skates discarded from the Greenland halibut gillnet fishery precludes us from determining what the actual relative losses due to discarding might be.

PREDATION

The abundance of juvenile skate has been above average throughout much of the 1990s and 2000s despite below average spawner abundance (Fig. 11). This suggests that juvenile mortality was relatively low during this period. In contrast, the below-average adult abundance throughout much of the 1990s and 2000s despite strong recruitment suggests that adult mortality was relatively high during this period. Stage-structured models fit to these data confirm this expectation, indicating that juvenile mortality had declined to a low level in the 1990s and 2000s and adult mortality had increased to a high level in these decades (D.P. Swain, unpublished analyses). Note that these models assume that smooth skate in the southern Gulf represent a closed population, or a constant proportion of a larger population, which may not be true. This pattern of declining mortality for small fish and increasing mortality for large fish is widespread throughout the marine fish community in the southern Gulf of St. Lawrence (Benoît and Swain 2008; Swain et al. 2009; Benoît and Swain 2011). An hypothesis that has been proposed to explain this widespread pattern is that small fish were released from predation when large demersal fish declined to very low levels of abundance in the 1990s due to overfishing, whereas the predation mortality experienced by large individuals increased to high levels in the 1990s due to the combination of their low abundance and the high abundance of an important predator, the grey seal (Benoît and Swain 2011; Fig. 20). Benoît et al. (2011) reviewed existing information on the possible role of other predators (fish, birds, other marine mammals) in explaining similar mortality trends estimated for southern Gulf winter skate. They concluded that grey seals were likely the most common predator of large winter skate and the most likely cause of elevated adult mortality. The evidence they reviewed is generally pertinent for thorny skate, though a detailed review is nonetheless warranted. Direct evidence for predation on smooth skate by grey seals is limited (but see Benoît and Bowen 1990), likely because consumed skates leave few hard parts (spines) in seal guts or scat.

ENVIRONMENTAL CHANGE

Temperature is the only dynamic environmental variable potentially affecting smooth skate for which there is a long and continuous time series. The deeper waters in which smooth skate occur warmed by close to 2°C from the late 1960s to 1980 (Fig. 21). Temperatures in the deep channels of the southern Gulf have fluctuated without trend since 1980. An effect of temperature change on smooth skate survival and abundance is therefore unlikely.

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Table 1. Commercial species and fisheries (defined by the gear class that is employed) included in the estimates of skate bycatch.

Species	Fisheries
Atlantic cod (<i>Gadus morhua</i>)	Fixed and mobile gear
Redfish (<i>Sebastes</i> sp.)	Mobile gear
Atlantic halibut (<i>Hippoglossus hippoglossus</i>)	Fixed gear
Greenland halibut (<i>Reinhardtius hippoglossoides</i>)	Fixed gear
White hake (<i>Urophycis tenuis</i>)	Fixed and mobile gear
American plaice (<i>Hippoglossoides platessoides</i>)	Fixed gear
American plaice and witch flounder (<i>Glyptocephalus cynoglossus</i>)	Mobile gear
Winter flounder (<i>Pseudopleuronectes americanus</i>)	Fixed and mobile gear
Yellowtail flounder (<i>Limanda ferruginea</i>)	Mobile gear
Spiny dogfish (<i>Squalus acanthias</i>)	Fixed gear
Shrimp (<i>Pandalus</i> sp.)	Mobile gear

Table 2. Summary of the fisheries and years for which estimates of bycatch are based on multiple years of pooled fisheries observer data. The years for which the data were pooled for the estimation are also indicated. For fisheries and years not listed here, relevant within-year data were used.

Fishery	Years for which pooled data were used	Years included in the pooled data
Cod (fixed gear)	1991 1993-1997	1991-1993 1991-1999
Dogfish	1991, 1992 2000-2006	1993-1995 1998-2006
Halibut	1991-1993, 1996, 1997	1991-1999
American plaice (fixed gear)	1991-1993, 1998-2007	1991-2010
Redfish	1998, 1999 2000-2010	1991-1999 2000-2010
Greenland halibut	1992	1991-1994
Winter flounder (fixed gear)	1991-2010	1991-2010
Winter flounder (mobile gear)	2006-2010	2000-2010
White hake	1991-1995	1991-1995
Yellowtail flounder	1991-1998 1999-2002	1995-1998 2000-2005

Table 3. Official skate landings for 1971-2010 and estimated landings (with lower and upper 95% confidence intervals, LCI and UCI respectively) for southern Gulf of St. Lawrence smooth skate (1991-2010). All values are in tonnes.

Year	Landings	Estimated		
		Mean	LCI	UCI
1971	8.00			
1972	2.00			
1973	3.00			
1974	132.00			
1975	131.00			
1976	43.00			
1977	5.00			
1978	12.00			
1979	17.00			
1980	22.00			
1981	66.00			
1982	1.00			
1983	35.00			
1984	0.00			
1985	0.00			
1986	3.00			
1987	0.00			
1988	1.00			
1989	1.00			
1990	0.68			
1991	4.19	0.58	0.17	0.95
1992	1.66	0.23	0.07	0.40
1993	7.98	1.05	0.44	1.77
1994	55.83	16.36	0.19	42.40
1995	32.74	4.49	0.46	13.10
1996	24.36	8.38	0.51	19.98
1997	9.55	2.68	0.25	7.58
1998	8.04	3.44	0.30	10.01
1999	11.17	3.04	0.81	5.99
2000	5.68	0.19	0.07	0.44
2001	3.61	0.86	0.04	1.85
2002	6.25	1.23	0.37	2.14
2003	9.86	3.95	1.79	6.85
2004	21.02	9.53	2.32	18.93
2005	13.88	5.63	0.77	12.96
2006	2.82	1.40	0.32	2.93
2007	1.85	0.38	0.02	0.98
2008	1.92	0.38	0.12	0.75
2009	5.32	1.50	0.01	4.65
2010	3.27	0.56	0.16	1.09

Table 4. Estimated discards (in tonnes, with lower and upper 95% confidence intervals, LCI and UCI respectively) for southern Gulf of St. Lawrence smooth skate (1991-2010).

Year	Mean	LCI	UCI
1991	92.35	51.99	137.27
1992	108.23	82.54	132.48
1993	91.79	55.43	140.11
1994	179.09	96.02	251.23
1995	77.24	46.04	120.66
1996	62.98	42.52	86.03
1997	81.42	46.99	130.37
1998	88.50	64.12	111.24
1999	78.01	61.57	97.84
2000	67.12	53.84	82.73
2001	38.31	27.89	51.17
2002	22.64	16.89	30.96
2003	33.41	25.36	42.22
2004	66.49	41.27	96.11
2005	55.40	39.79	74.42
2006	46.03	34.04	60.65
2007	22.87	15.11	32.27
2008	34.20	23.98	47.84
2009	27.35	20.19	35.78
2010	23.68	16.65	34.46

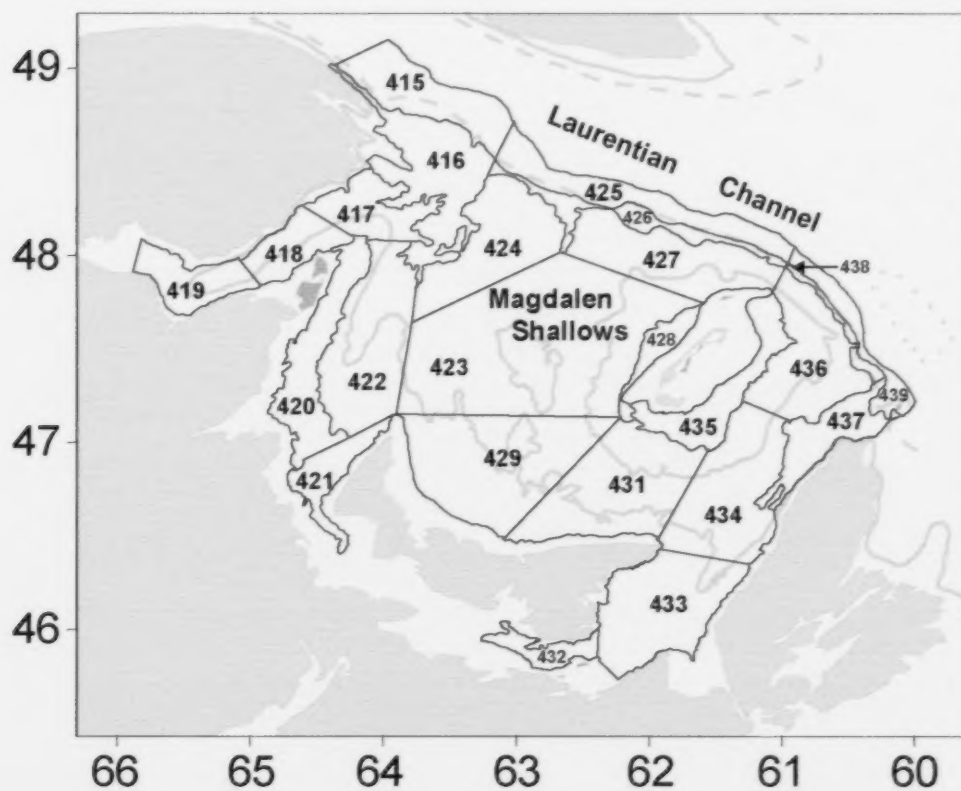


Figure 1. The southern Gulf of St. Lawrence, showing strata used since 1971 in the annual September bottom-trawl survey. Depth contours: solid grey line = 60 m; dashed grey line = 200 m; dotted grey line = 500 m.

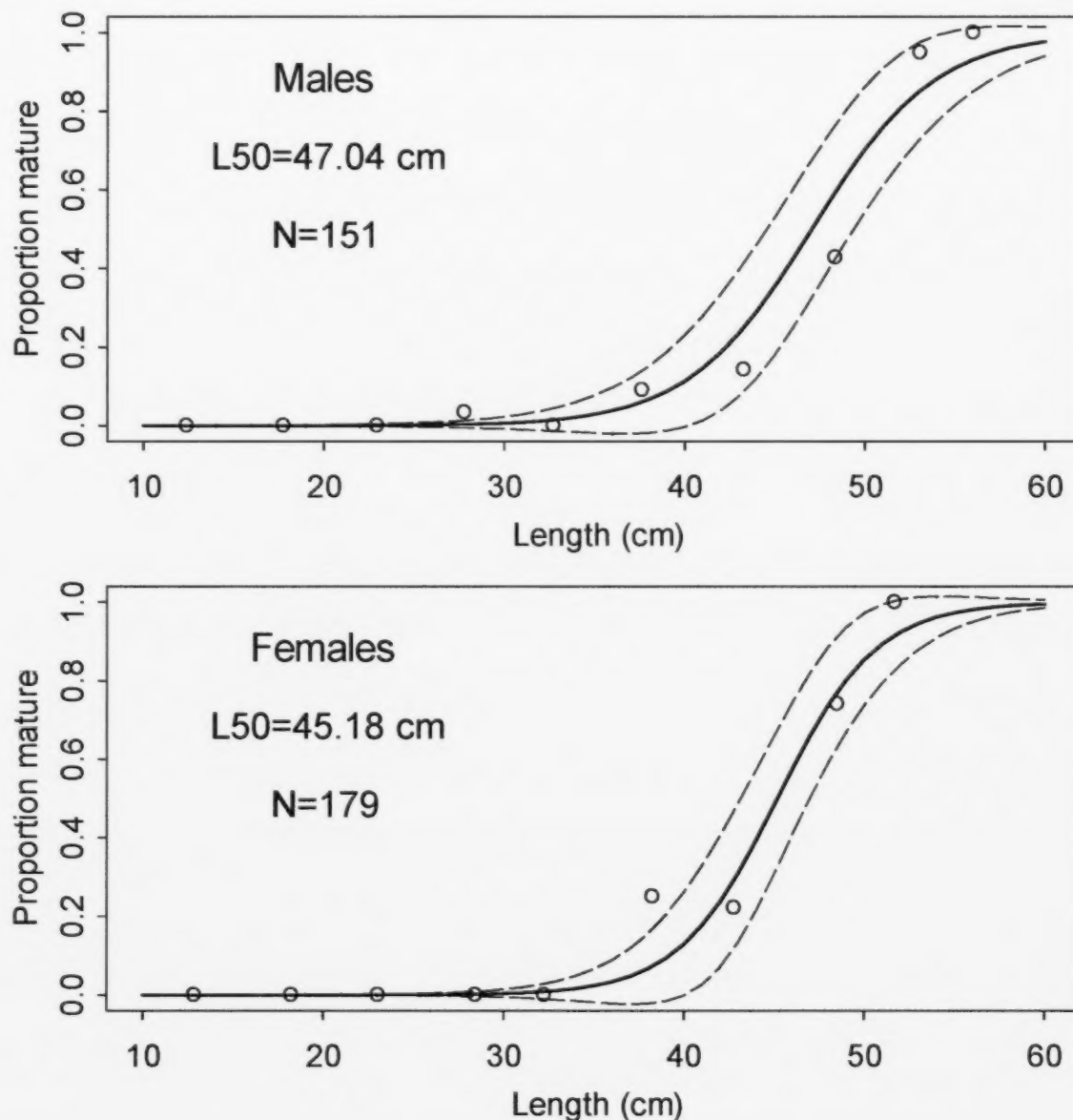


Figure 2. Length at maturity for smooth skate in the southern Gulf of St. Lawrence, 2005-2009. Solid lines show the predicted proportion mature based on a logistic regression model and dashed lines are ± 2 SE. L_{50} is the length at which 50% of skates are predicted to be mature based on the coefficients of the fitted logistic regression. N is the sample size, and circles show the proportion mature in 5-cm length bins.

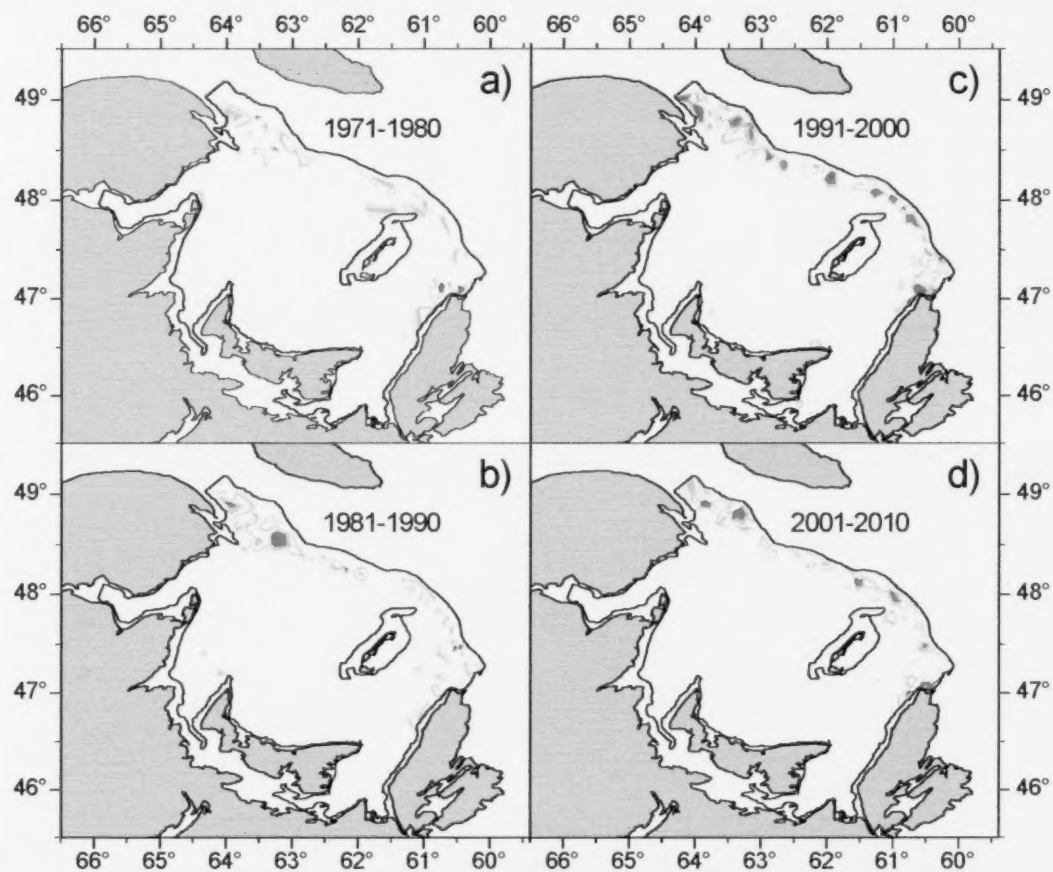


Figure 3. Geographic distribution of smooth skate catches in the September survey of the southern Gulf of St. Lawrence. Contours intervals are the 10th (blue), 25th (green), 50th (yellow), 75th (orange) and 90th (red) percentiles of nonzero catches (fish/tow over the 1971-2010 period).

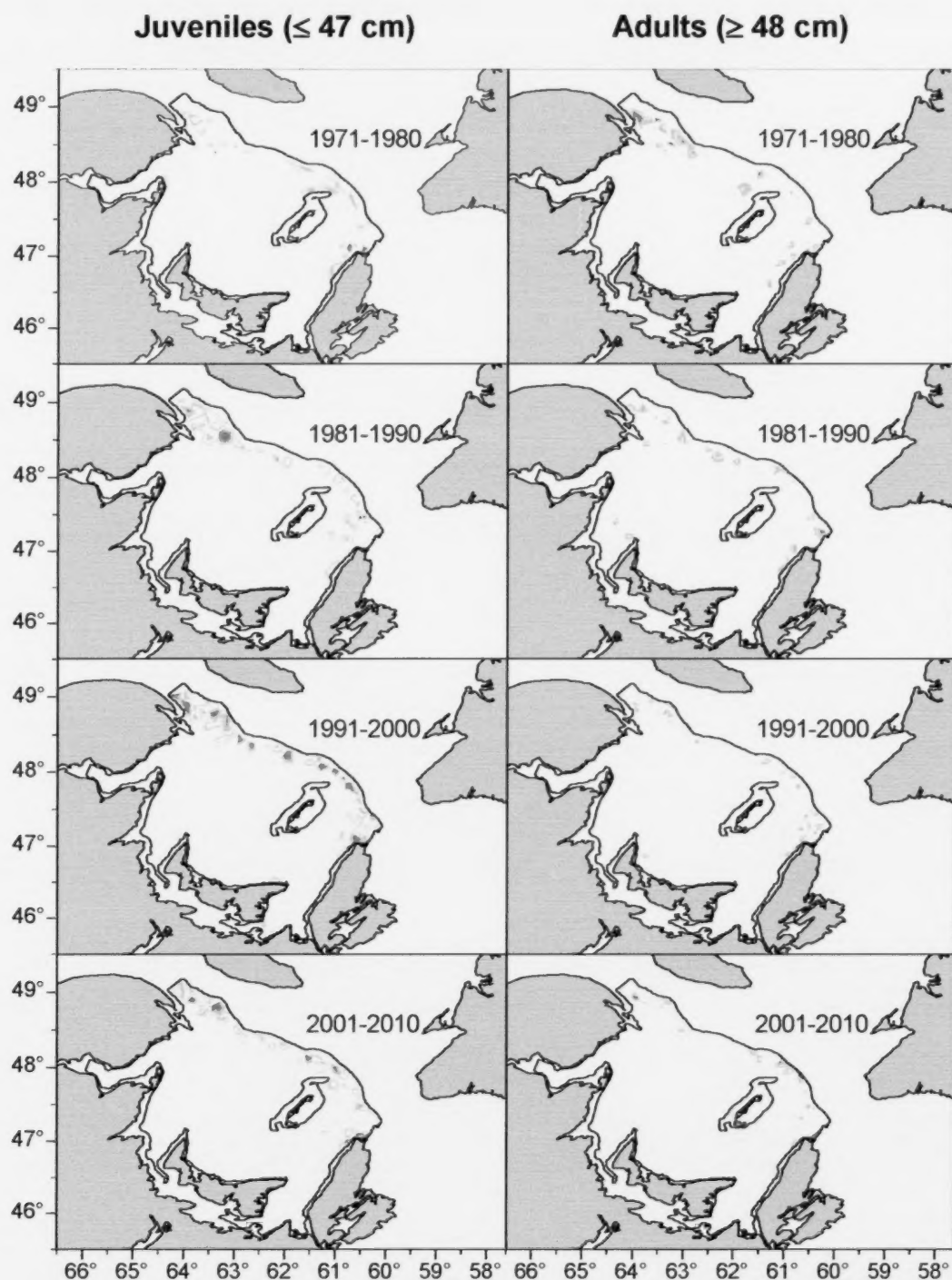


Figure 4. Geographic distribution of juvenile (<48 cm TL) and adult (≥ 48 cm TL) smooth skate catches in the September survey of the southern Gulf of St. Lawrence. Contours intervals are the 10th (blue), 25th (green), 50th (yellow), 75th (orange) and 90th (red) percentiles of nonzero catches (fish/tow).

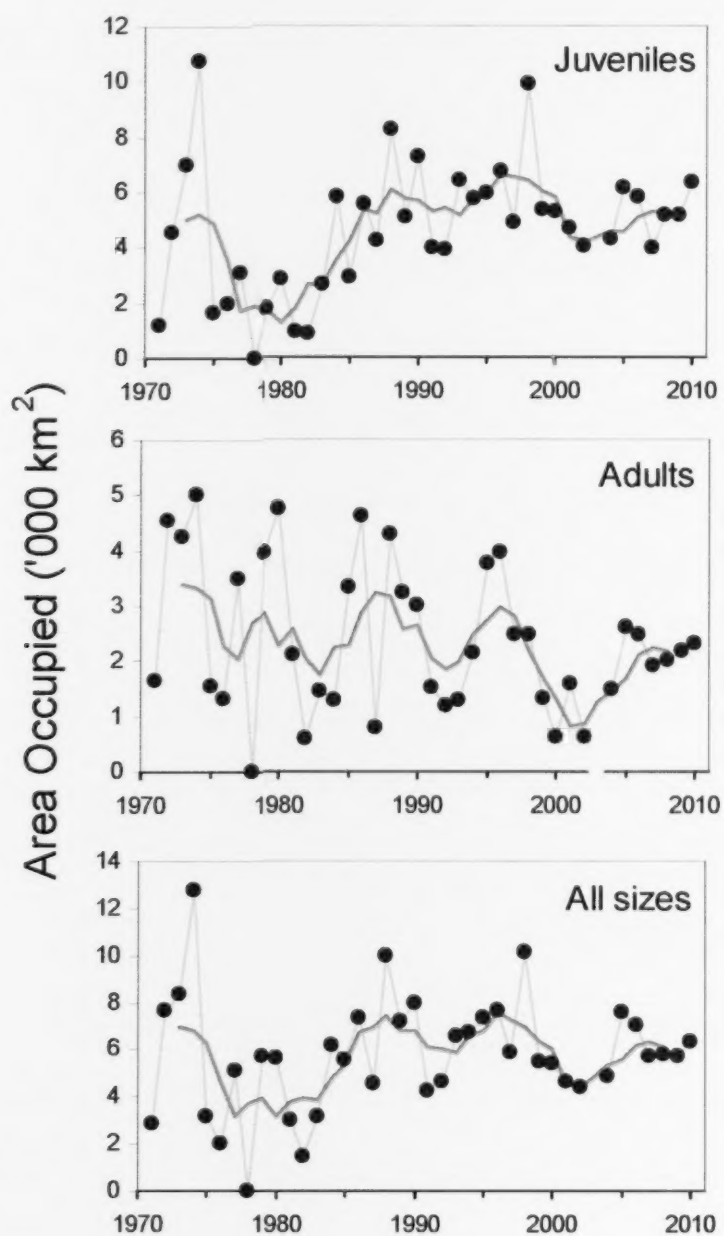


Figure 5. Area occupied by three size classes of smooth skate in September in the southern Gulf of St. Lawrence, 1971-2010. Heavy line is a 5-yr moving average. The juvenile and adult size classes consist of skates ≤ 47 cm and ≥ 48 cm in length, respectively.

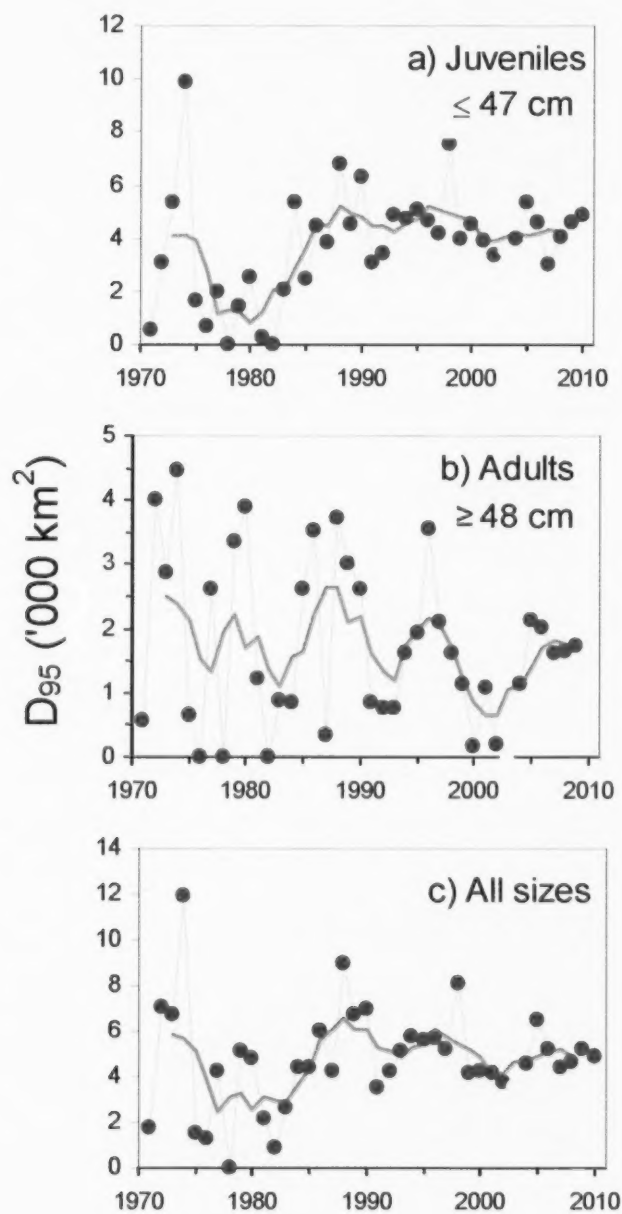


Figure 6. Time trend in an index of geographic range (D_{95}) for three size classes of smooth skate in September in the southern Gulf of St. Lawrence. Heavy line is a 5-yr moving average.

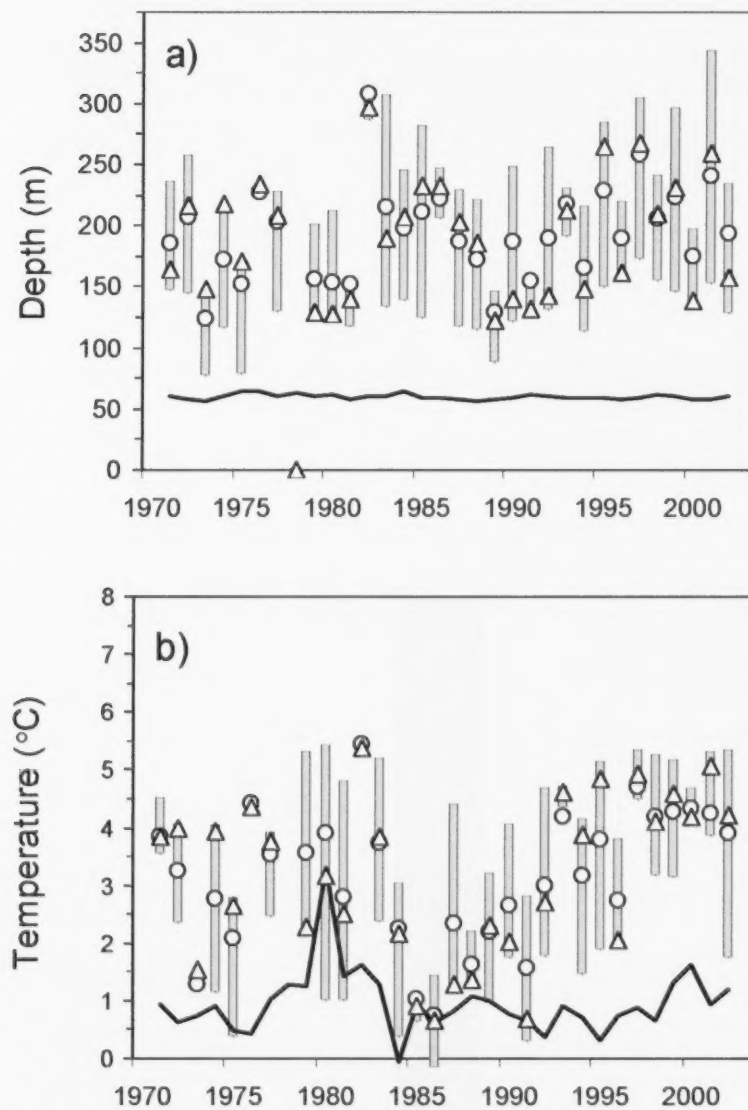


Figure 7. Associations of smooth skate with a) depth and b) temperature in September in the southern Gulf of St. Lawrence. Line shows the median depth or temperature available in the sampled area. Circles and triangles show the mean and median depth or temperature occupied by smooth skate. Bars show the 25th to 75th percentiles of occupied depths or temperatures. Near-bottom temperatures were not available for depths greater than 155 m in the shaded years in panel b (1984-1988).

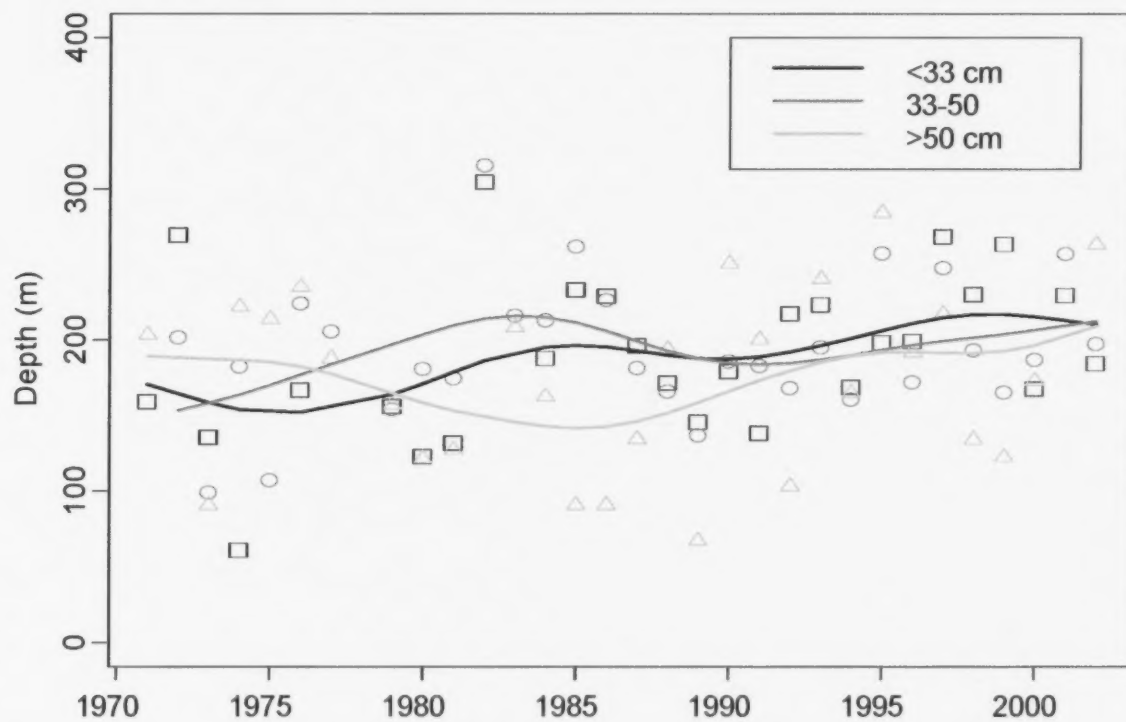


Figure 8. Mean depth occupied by three length classes of smooth skate in September in the southern Gulf of St. Lawrence.

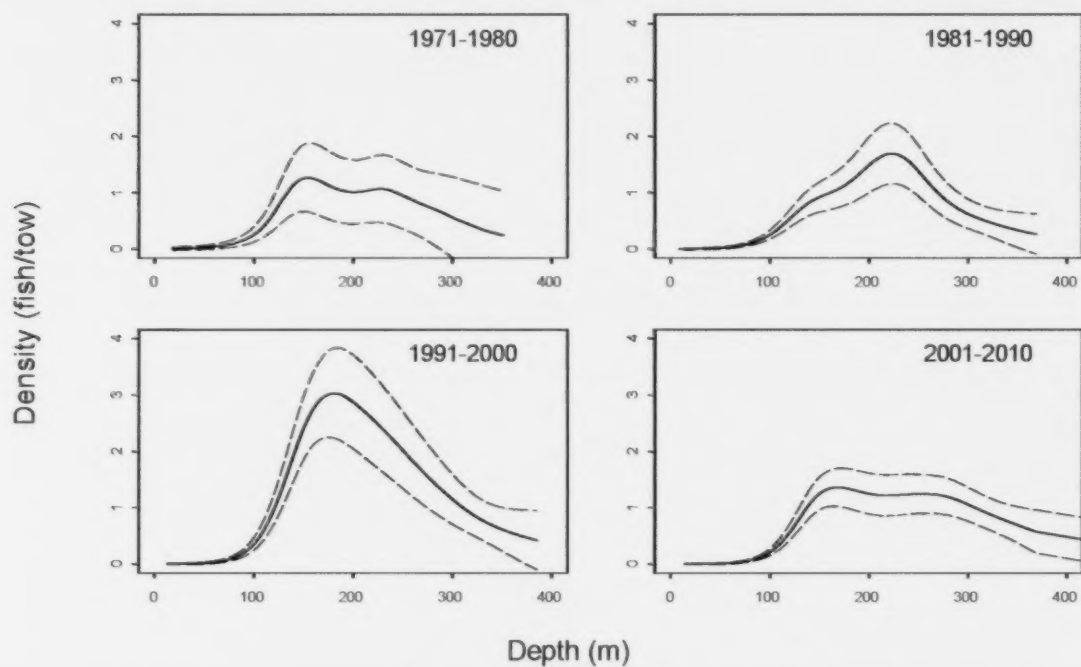


Figure 9. Effect of depth on the local density of smooth skate in September in the southern Gulf of St. Lawrence in four time periods. Heavy lines show the fitted relationship, and shaded bands are $\pm 2SE$.

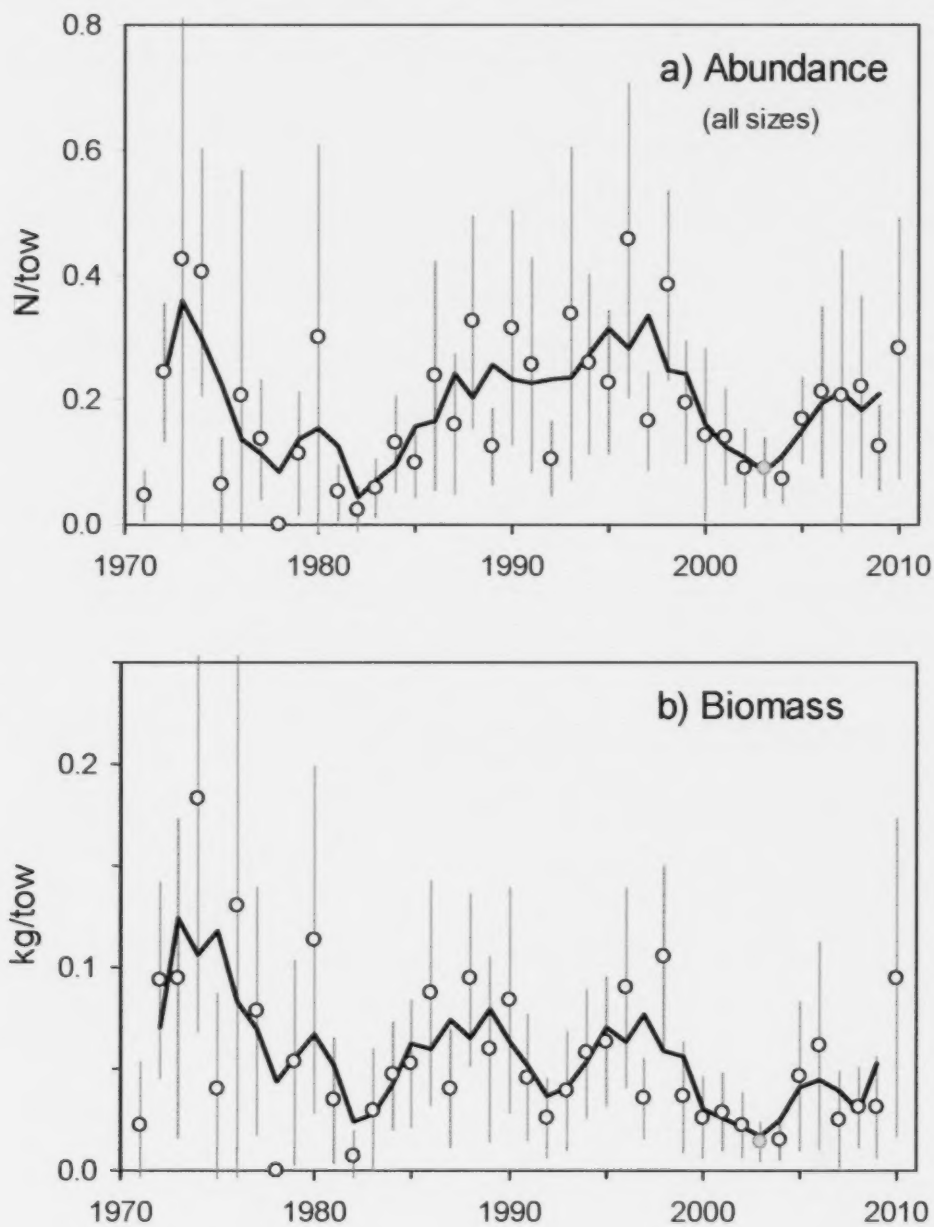


Figure 10. Stratified mean catch rates of smooth skate (all sizes) in the September survey of the southern Gulf of St. Lawrence. Vertical lines are $\pm 2SE$. Heavy lines show 3-yr moving averages. Catch rates are adjusted to daytime catchability. The grey circles denote the catch rates from 2003 survey, which was conducted by an uncalibrated vessel (the Wilfred Templeman).

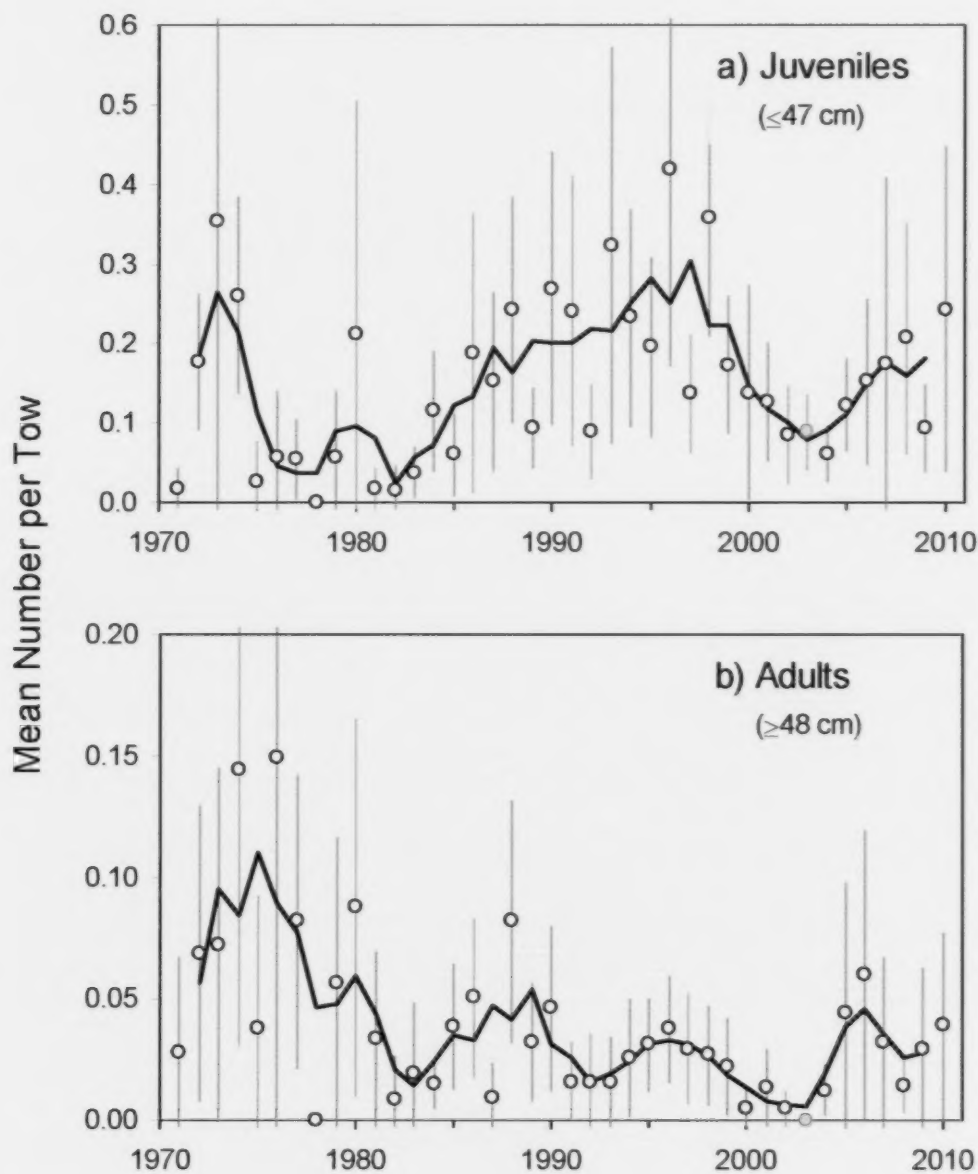


Figure 11. Stratified mean catch rates of juvenile and adult smooth skate in the September survey of the southern Gulf of St. Lawrence. Vertical lines are $\pm 2SE$. Heavy lines show 3-yr moving averages. Catch rates are adjusted to daytime catchability. The grey circles denote the catch rates from 2003 survey, which was conducted by an uncalibrated vessel (the Wilfred Templeman).

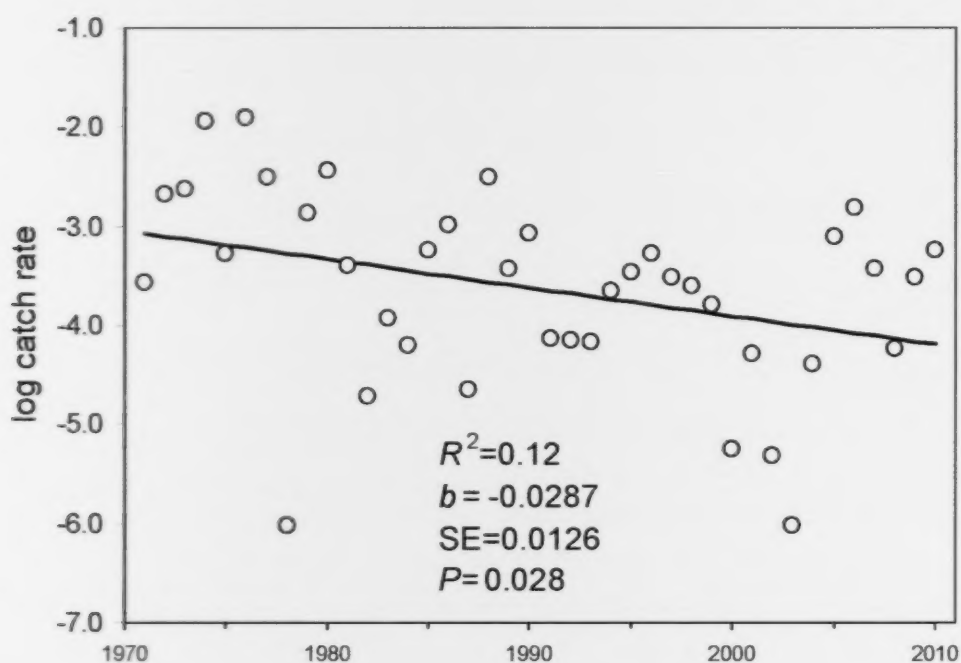


Figure 12. \log_e -transformed catch rates of adult (≥ 48 cm TL) smooth skate in September surveys of the southern Gulf of St. Lawrence. Line shows the regression of \log_e catch rate on year.

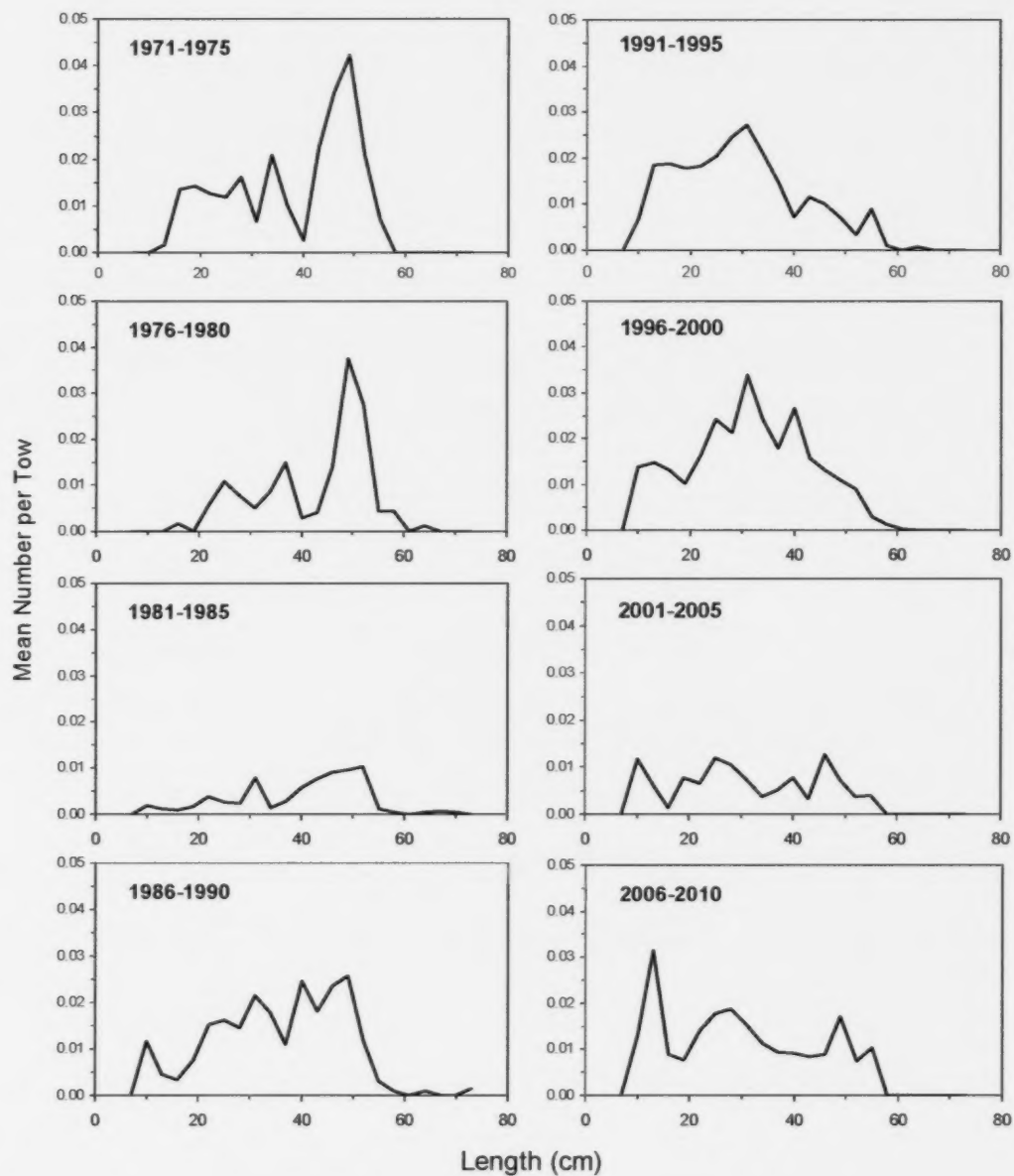


Figure 13. Stratified mean length frequency distributions of smooth skate in the southern Gulf of St. Lawrence in September in 5-yr blocks.

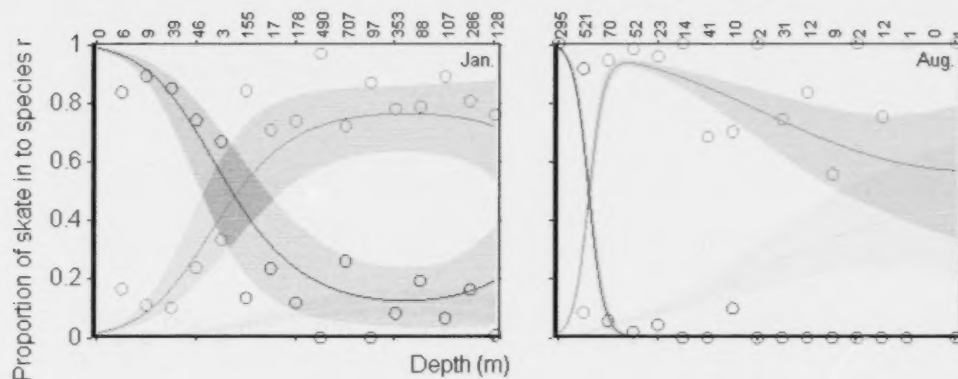


Figure 14. Examples of the fit of the multinomial harmonic regression model for two months, January (left panel) and August (right). Observed (circles) and predicted (lines, with the 95% confidence band denoted by shading) relative proportions of the three sGSL skate species (thorny skate, red; smooth skate, green; winter skate, blue) are shown as a function of depth. Survey catches were summarized in depth bins of 25 m for plotting. The numbers above each panel indicate the number of individual skate from a particular depth and time bin that were used to fit the model.

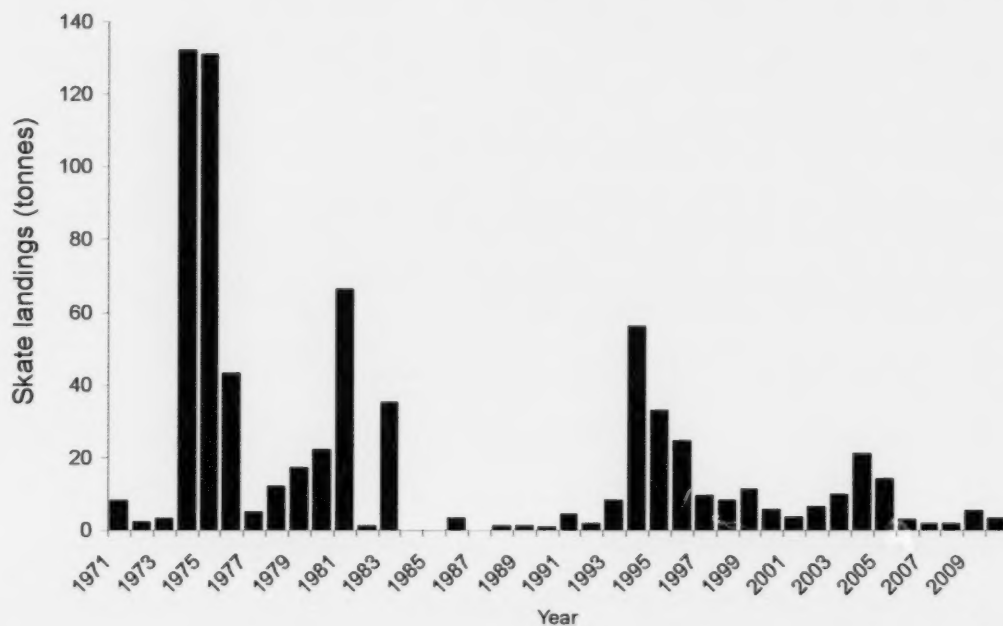


Figure 15. Landings of skates in the southern Gulf of St. Lawrence (NAFO 4T), 1971-2010.

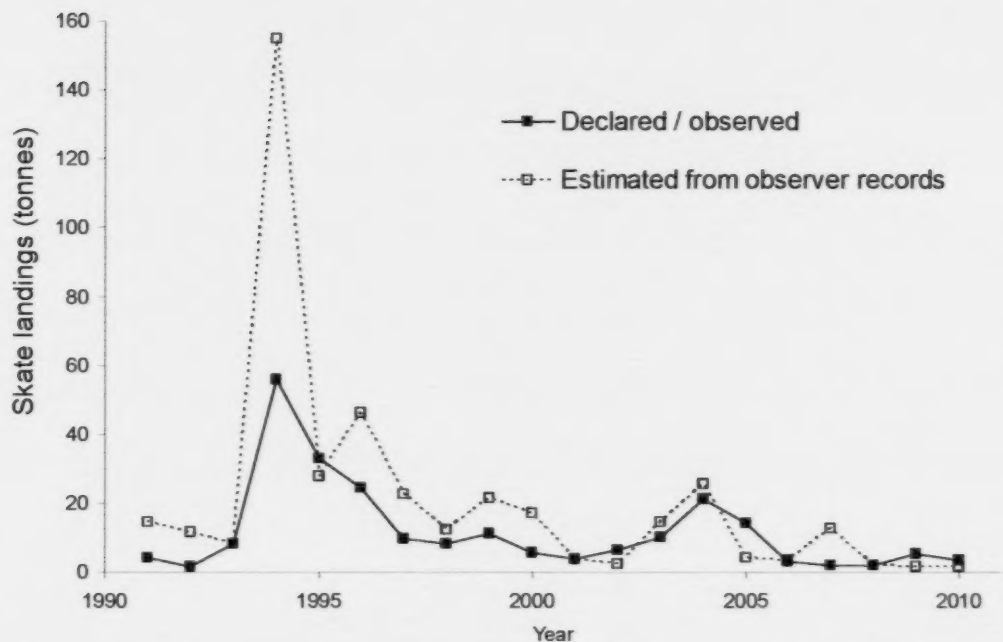


Figure 16. Official landings of skates (based on declared catches or dockside catch observation) and landings estimated using the amount of retained skates reported by fisheries observers, for NAFO division 4T.

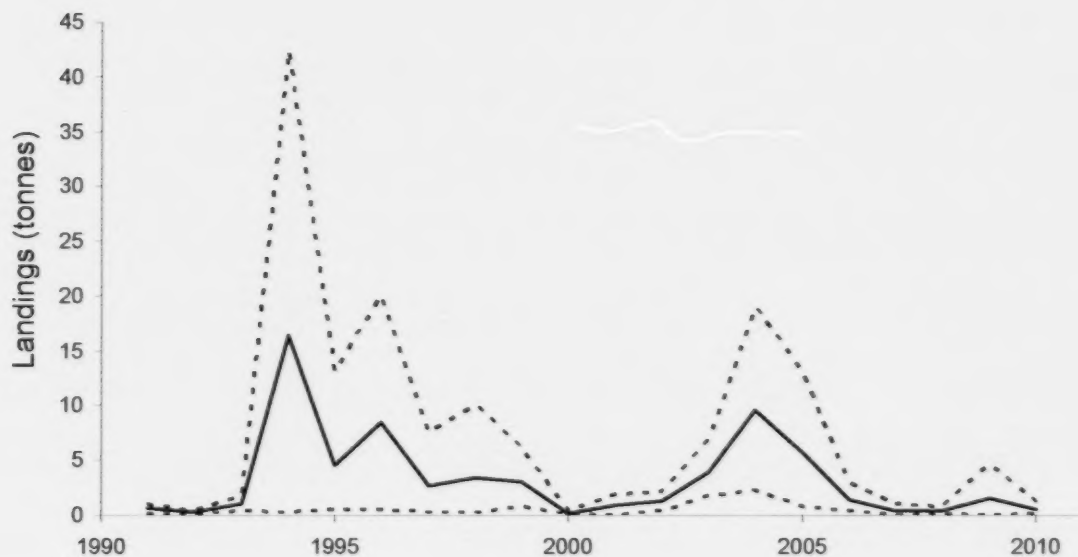


Figure 17. Estimated landings of smooth skate based on the multinomial harmonic regression model (with 95% confidence interval indicated by the dashed lines), 1991-2010.

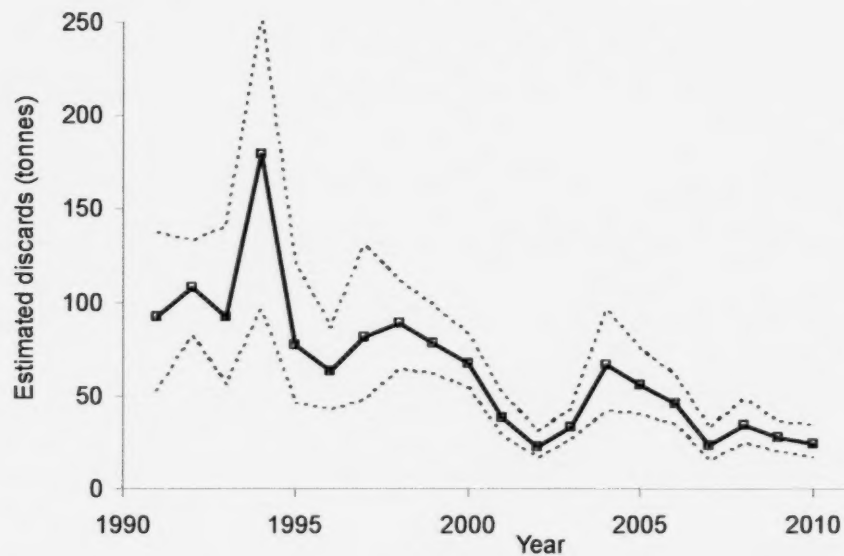


Figure 18. Estimated discards of smooth skate (with 95% confidence interval indicated by the dashed lines), 1991-2010.

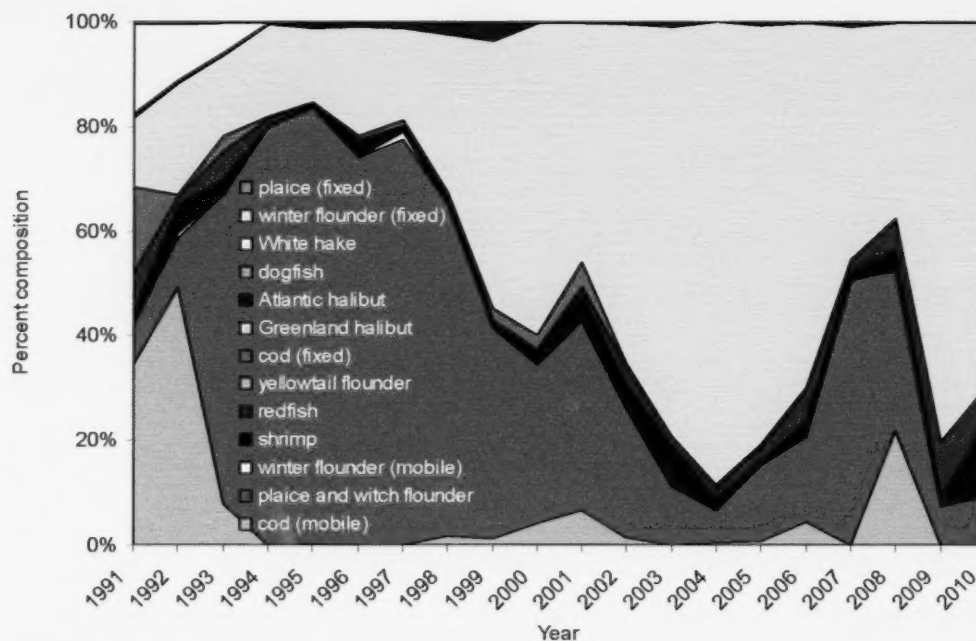


Figure 19. Relative contribution of different sGSL fisheries to smooth skate discards, 1991-2010

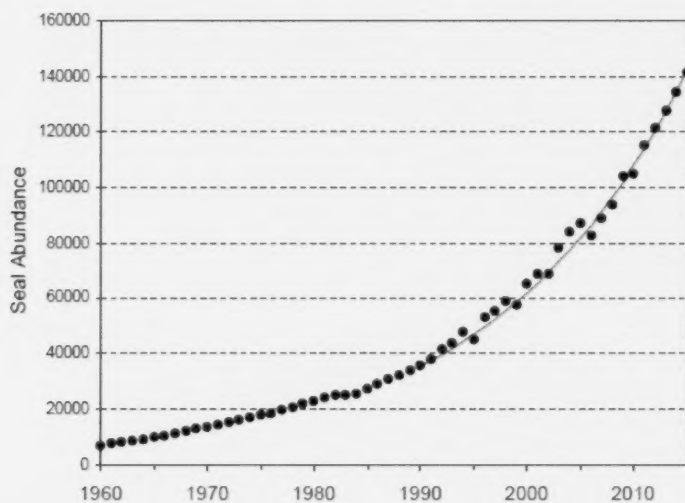


Figure 20. Estimated abundance of grey seals occurring at some time of the year in the southern Gulf as well as the neighbouring Sydney Bight area during winter (December-April).

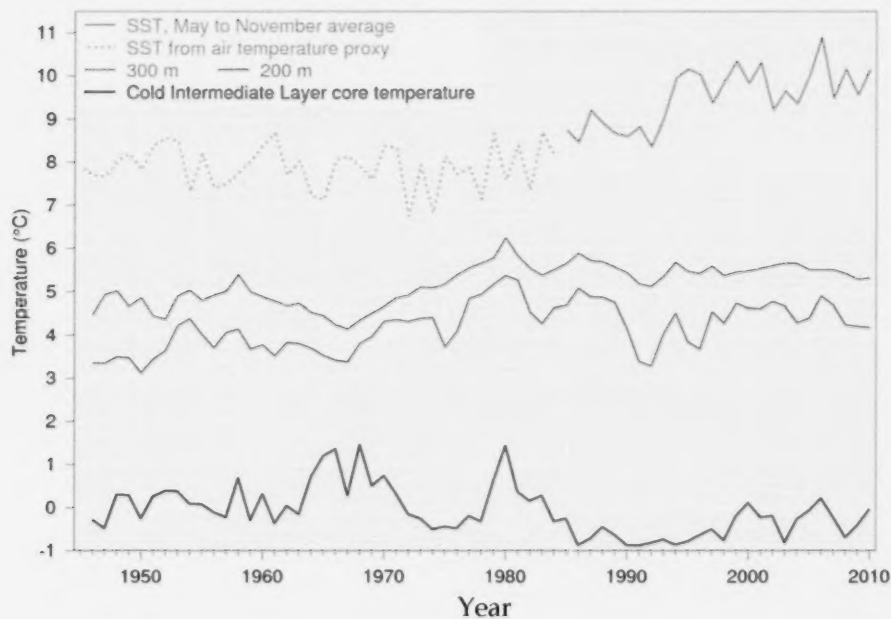


Figure 21. Water temperatures in the Gulf of St. Lawrence. May-November sea surface temperature (SST) averaged over the Gulf (1985–2010, red line), completed by a proxy based on April–November air temperature (1945–1984, red dashed line). Layer-averaged temperature for the Gulf of St. Lawrence at 200 and 300m (green lines). Cold intermediate layer minimum temperature index in the Gulf of St. Lawrence (blue line). SST from Galbraith et al. (2012), and other time series from Galbraith et al. (2011). Figure courtesy of P. Galbraith (DFO, Quebec Region).

Appendix I: Skate maturity stages

Code	Stage	Male	Female
1	Immature	Claspers are undeveloped, shorter than extreme tips of posterior pelvic lobes. Testes small, thread shaped.	Ovaries small, with their surface undeformed and smooth. No eggs visible on the dorsal or ventral surface. Ovary thinner than stage 2.
2	Maturing 1	Claspers are more or less extended, longer than tips of posterior pelvic lobes. Their tips (glans) are more or less structured, but their skeleton is still flexible, soft. Testes are enlarged, sperm ducts beginning to meander.	Clear eggs up to 2 millimeters in diameter are visible in the top surface (dorsal) of the ovaries. Surface of ovaries smooth and undeformed. Caution: When observing from the ventral surface the ovary must be flipped over.
3	Maturing 2	No stage.	Eggs grow in size (2-5 mm) and are cream coloured. Texture and content resemble small chicken yolks except for colour. Dorsal surface of ovary irregular. Ventral surface of ovary may still be smooth in early stage but slicing ovary with knife immediately reveals eggs.
4	Mature	Claspers full length, glans structure fully formed, skeleton hardened so that claspers are stiff. Testes greatly enlarged, sperm ducts meandering and tightly filled with flowing sperm.	Eggs grow in size (5-20 mm) and turn chicken yolk creamy yellow in colour and texture. Ovaries swollen and deformed on all surfaces. Blood vessels appear on yolk surface in later stage. Yolk may be seen in the fallopian tubes.
5	Spawning	Glans often dilated, its structures reddish and swollen. Sperm present in clasper groove or glans and flows on pressure from the cloaca.	Yolk in fallopian tubes beginning to be enveloped by purse. This begins at the rear and continues until entire yolk is surrounded by purse. The number of purses should be noted in comments. When complete the purse is discharged.